THE SELECTION OF SEED SIZE BY FINCHES

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Theories dealing with ecological aspects of species formation in birds and diversity within avian communities have used ratios of culmen lengths as indices of the disparity between the niches of sympatric congeneric species (Klopfer and MacArthur, 1961). The use of such indices assumes, in most cases, a relation between the size or shape of a bird's bill and the size and shape of the food it eats; Snow (1954) has even gone so far as to correlate particular bill types with particular habitat types. This assumption, although frequently made, has never been satisfactorily demonstrated experimentally. Two recent studies have shown that different bird species feed on different sizes of food in the wild: Bowman's study of congeneric species (1963) is discussed below; Gibb (1956) has shown that unrelated species will feed on different sizes of the same food, but did not discuss the role of bill size and shape which is complex in his case.

The present study was undertaken with the idea of investigating the morphological determinants of feeding from a simple experimental standpoint. In general, one may visualize a bird's feeding as involving four steps: the psychological choice of food, its acquisition, preparation for swallowing, and digestion. Experiments were designed to test the first and third of these—that is, to show that birds of two different species with different bill sizes would not only choose different sizes of the same food, but also feed more efficiently on them. Kear (1962) has already shown that different bird species of the same family will choose and feed more efficiently on different sorts of food; Bowman (op. cit.) has shown that congeners will feed on different sizes of different foods. The role of the factors of taste or nutritional preferences, as well as of differences in the degree of difficulty in husking different seed types, could not be readily assessed in either study. Consequently, the study below used only different sizes of the same food, thus allowing analysis of the mechanical aspects of feeding alone.

MATERIALS

The species used were the White-throated Sparrow (*Zonotrichia albicollis*) and the Slate-colored Junco (*Junco hyemalis*), individual subjects being trapped from populations wintering in North Carolina. Drawings of the bills of the two species are given in Figure 1. The shapes are basically the same, although the culmen of the junco is somewhat more convex at the tip (see Bowman, 1961:141ff., for a discussion of bill shape). The differences in the size of the bills are given in Table 1. The ratio of the larger culmen measure-

FIG. 1. Drawings of bills of test species (not to scale).

ment to the smaller is small, that of the larger depth to the smaller being somewhat greater. The unequal difference in bill depth as compared to length is probably more important than the length itself in determining the demonstrated differences in feeding; the advantage of a relatively deeper bill of the same shape has been summarized by Bowman (1961:153f.). No single dimension can be used, a priori, as an index of differences in feeding.

TABLE 1
MEASUREMENTS OF TEST SPECIES

Measurements*		Junco	Whitethroat	Ratio: Whitethroat/Junco
Net length (without tail)	mm	79.7 (56)	85.8 (14)	1.08
Bill: Exposed culmen	mm	11.0 (56)	11.4 (14)	1.04
Depth at base	mm	6.3 (39)	7.7 (14)	1.22
Weight	g	21.1 (856)	27.1 (347)	1.28
Ratios—				
Culmen/length		0.138	0.133	0.96
Depth/length		0.079	0.090	1.14

* Linear measurements taken from Ridgway (1901); all are averages of male and female averages, those of the junco for all subspecies. Sample size given in parentheses; Ridgway seems not to have measured all junco specimens for depth of bill. Weights from Helms (1963); the mean fat class of the species differed by only 5 per cent. The ratio of the cube roots of the weights was 1.078, negligibly different from the ratios of the adjusted lengths.

TABLE 2
WEIGHTS OF SUNFLOWER SEEDS*

Size class (mm)	Sample 1 Shell (g)	Sample 1 Kernel (g)	Sample 1 Total (g)	Sample 2 total (g)	Difference (per cent)
9–11	0.957	1.184	2.141	2.085	−3
11–13	1.015	1.311	2.326	2.235	−4
13–15	1.313	1.744	3.057	2.957	−3
15–17	1.682	1.988	3.663	3.774	+3

* Each measurement is the total weight of 25 seeds; only the total weights were measured in the second sample.

In the tests only sunflower seeds were used, because they were the only seed type readily available that both had a husk and was large enough to exhibit measurable size differences. The seeds were individually measured and assigned to one of four size (length) classes: 9 to 11, 11 to 13, 13 to 15, and 15 to 17 mm, seeds of exactly 11, 13, or 15 mm being discarded. Table 2 gives the average weight of kernel and husk for 25 seeds of each class; the totals of this sample compared with those of a second such sample differ regularly by a factor of only 3 per cent and not always in the same direction. The way both species open the seeds suggests that the thickness of the seed is, in fact, the most important dimension to the birds. The seed is held crosswise in the bill at the thickest portion of the seed and billed vigorously, being rotated occasionally so that the longer end of the achene sticks out of first one side of the bill and then the other. Both species opened the seeds in this way.

As noted, the midrange values were assigned to the seed size classes: none of the measurements were recorded nor averages made. It can be shown that the mean lengths of the seeds in the longest and shortest size classes were shorter and longer, respectively, than the midrange values expected. This result might have been predicted in view of the difficulty in obtaining seeds from these classes; this means that in the graphs (Fig. 2) the spacing of the seed classes on the abcissa is not equal, and the two extreme classes are closer to the middle two than shown.

CHOICE EXPERIMENT—PROCEDURE AND RESULTS

Three birds of each species were used. These were placed all at once in a small room roughly 8 by 12 feet in size. The two species were kept separate by a net partition along the long axis of the room. The birds had prior experience with the four seed sizes, both separately as their only food for some periods and mixed with their regular seed mixture at others (cf. Kear, op. cit.). The birds were then presented with a choice situation in which 200 seeds, 50 of each of the four sizes, were offered as the only food for six-hour

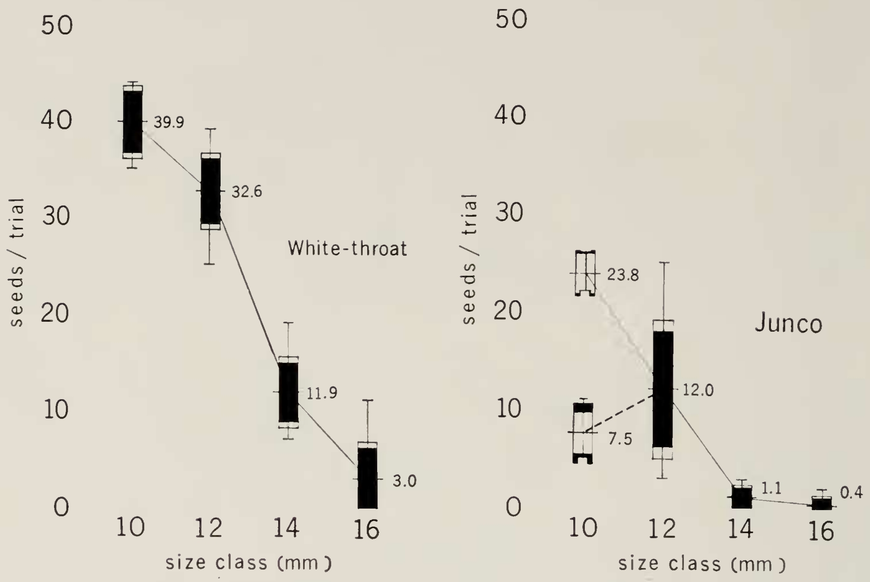

Fig. 2. Average seed consumptions, out of 50 seeds offered, for eight tests. The vertical line gives the range; the open vertical band, the standard deviation; the closed vertical band the 95 per cent confidence interval of the mean; the horizontal line, the mean. The upper figure of the smallest junco seed class is for the first four tests; the lower, for the second four tests.

periods. The seeds were placed in four separate cups on the inside of a special feeding dish that allowed only one bird to feed at a time; thereby peck-order relationships were prevented from affecting preference. At the ends of these periods all shells and uneaten seeds were removed and the number eaten calculated. A mixture of different sorts of seeds was used as food between tests. Two series of four tests were run; the results are given in Figure 2. The results require a qualification with respect to the drop in consumption of the smallest seeds by the juncos in the second series of tests. The smallest seeds used in this series of tests had been taken from a newly bought batch of seeds because of the scarcity of seeds of this size class in the original material. The new seeds were noticeably different in shell markings from the original material and showed no air space, present in the first seeds between the seed coat and the kernel. Apparently this closeness made the shells too difficult to open. This interpretation is supported by the fact that the drop occurred in this class alone and, surprisingly, was not balanced by an increase in consumption of larger seed types: the Whitethroats were not affected.

TABLE 3
KERNEL EXTRACTION TIMES OF WHITE-THROATED SPARROWS

Size class (mm)	Number observations	Mean (min)	Range (min)	Standard error (min)
9–11	20	1.22	0.23–4.85	0.255
11–13	20	1.43	0.37–3.50	0.205
13–15	14	2.01	0.33–3.88	0.288
15–17	13	2.38	0.58–5.02	0.383

EFFICIENCY EXPERIMENT—PROCEDURE AND RESULTS

The birds' efficiency in extracting the seed for swallowing was measured by observing the time taken by two White-throated Sparrows to husk individual seeds of each of the four size classes. A single bird was isolated on one side of the experimental room and fed with seeds of a single size class. The bird was observed through one-way glass and timed from when he picked up and began billing the seed to the time he hopped away from, or stopped paying attention to, the empty shells. The time the bird is occupied in extracting the seed—and thus prevented from any other feeding—is considered more significant than just the time taken to break the shell (cf. Kear, op. cit.). The extraction times, measured in minutes, are given in Table 3. One bird was observed for 10 scores in each of the four size classes; the other bird was used for the rest of the scores, escaping before the full 40 scores could be obtained. Although over 12 hours of observations were made, only six scores could be obtained for juncos so that conclusions on efficiency must be drawn from the Whitethroat scores alone. (The junco scores were, for 9–11 mm seeds, 0.92, 3.37, and 7.13 minutes; for 11–13 mm seeds, 0.77, 2.97, and 4.55 minutes. These scores are higher, on the average, than those of the Whitethroats.)

Because of the large variance in the Whitethroat scores, a linear regression was run on the data to determine whether or not the observed increase in extraction scores with seed size was significant. A slope of $b_{yx} = 0.36$ was obtained with 95 per cent confidence intervals of $\pm$ 0.22. This value of the slope may be low since the midrange value assigned as the value of x was too high and low for the largest and smallest seed classes as discussed above.

DISCUSSION

The major structural difference of the Whitethroat bill from that of the junco is that it is relatively deeper. The data from the choice experiment and the few junco husking scores indicate that the Whitethroat feeds more easily on sunflower seeds than does the junco. The Whitethroat test individuals on the average ate 2½ times as many seeds of all classes in a six-hour period as the junco. The junco took 64 per cent of its seeds from the smallest class and only 4 per cent from the largest two, whereas the Whitethroat ate 45 per cent from the smallest and 17 per cent from the largest two. For the Whitethroat the sharp decrease in seeds chosen and sharp increase in husking times came between the 12- and 14-mm seeds, although, as noted previously, the difference in average seed size between these intermediate classes was probably greater than that between either the 10- and 12-mm or 14- and 16-mm classes. The possibility does exist that the choice curve is somewhat higher in the relative proportion of the second seed size taken by the Whitethroat because of the limiting of the amount of seed in the tests to only 50 per class; that is, the birds may have been forced to eat the larger seed when the supply of the smaller was exhausted. For the junco the inflection seems to lie within the 12-mm class, hence the wide variance in that class in the choice trials.

Kernel intake efficiencies were obtained by dividing the kernel weights of the seed classes (Table 2) by the husking scores (Table 3). When a linear regression is run on the resulting values, however, the slope is not significant, having a value of b_{yx} on the order of -10^{-6}. Although the slope of the husking scores was significant, because both they and the kernel weights were increasing with the length of the seed, the resulting quotient is not. A greater number of observations might show a significant slope.

The working hypothesis is that each species is adapted to feed most efficiently on an optimal seed size that is in some way related to the size and shape of its bill. That there is no obvious increase in efficiency of kernel intake with decreasing seed size for the Whitethroat is somewhat surprising, although all the seeds used in the experiment are larger than the normal seeds in the diet of the Whitethroat, and an increase in efficiency could well occur in a smaller size class than any tested in these experiments. Studies in progress on the food size of flycatchers, swallows, and vireos indicate that such optima do exist. It has been suggested by Dr. John Smith (pers. comm.) that differences in feeding technique, and, of course, habitat, not investigated here, are the primary means for niche separation in the case of the Whitethroat and junco.

SUMMARY

The frequent assumption that the size of a bird's food is correlated with the size and shape of its bill is supported by experiments on food choice and feeding time. In the first experiment White-throated Sparrows (large-billed species) and Slate-colored Juncos (small-billed species) were fed different sizes of the same food in a choice situation: in the second experiment the time taken to extract the kernel of each of the seed size types was measured for White-throated Sparrows. Two aspects of the feeding are shown: (1) that the relative choice of different sizes of the same seed is different for the two

bird species of different bill size, in a way predictable by the bill size; and (2) that choice of seed types by one of these species is generally correlated with the bird's speed in opening these types.

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LITERATURE CITED

Bowman, R. I.
1961 Morphological differentiation and adaptation in the Galapagos finches. *Univ. California Publ. in Zool.*, 58.
1963 Evolutionary patterns in Darwin's finches. *Occas. Papers California Acad. Sci.*, 44:107–140.

Gibb, J.
1956 Food, feeding habits and territory of the Rock Pipit *Anthus spinoletta*. *Ibis*, 98:506–530.

Helms, C. W.
1963 Tentative field estimates of metabolism in buntings. *Auk*, 80:318–334.

Kear, J.
1962 Food selection in finches with special reference to interspecific difference. *Proc. Zool. Soc. London*, 138:163–204.

Klopfer, P. H., and R. H. MacArthur
1961 On the causes of tropical species diversity: Niche overlap. *Amer. Nat.*, 95: 223–226.

Ridgway, R.
1901 The birds of North and Middle America. *U.S. Natl. Mus. Bull.*, 50, pt. 1:278–283, 343–346.

Snow, D. W.
1954 The habitats of Eurasian tits (*Parus* spp.). *Ibis*, 96:565–585.

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